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Archenema, protonema and metanema.

CONWAY MACMILLAN.

It is intended in this brief paper to call attention to certain gametophytic differentiations and possible homologies which, while not by any means everywhere overlooked, have not, perhaps, received the proper accentuation in current botanical thought. At the outset it may be well to attempt to give a definition of a gametophyte. As understood by the writer, this term does not by any means properly apply to every plant structure that produces gametes. The Cœloblasteæ, for example, mature undoubted eggs and sperms, but the plant body thus functioning can scarcely be termed a gametophyte. A gametophyte can be defined only in terms of a sporophyte held in contradistinction with it. Therefore it is only in that group of plants that I have named the Sporophyta[1] that gametophytic structures may be rightly discerned. It is inadmissible to apply the term to any plant below the position of Œdogonium (or Ulothrix?). A gametophyte, then, is a structure derived directly or indirectly from a sporophytic spore or its analogue, and itself capable of producing, directly or indirectly, a gamete or gametes. The algæ Œdogonium and Coleochæte, "leafy moss plants," fern prothallia, the endosperm of Araucaria, the pollen tube of Burmannia and the embryo-sac nuclei of Narcissus are types of gametophytes. The definition, it will be observed, takes note both of formation and of function. In the case of each a reservation must be made, for gametophytes may arise directly by propagative methods, as in the breaking up of a moss protonema, or by the activity of certain bodies (the homologies of which may be with multiple spores rather than with propagative structures), such as the gemmæ of Aulacomnium and Lunularia. And on the other hand, through apogamy, as in *Todea africana*, *Pteris cretica* and a few other ferns, or in some less aberrant manner, the gametophytic structure may fail to produce gametes.

Thus defined, the gametophyte may be isolated for study in any species where it occurs. It should be noted, perhaps,

[1] Metaspermæ of the Minn. Valley 20. 1892.

at this point, that the interlocking and interdependence of sporophyte and gametophyte is such that, wherever they alternate, certain structures appear, under a rigid classification, to be included in both categories. The same cell may be morphologically sporophytic but physiologically gametophytic, or *vice versa.* This is true of the two unicellular stages which serve to distinguish so sharply the higher plants from the higher animals (in which there is but one unicellular stage in the life-history of the organism). The spore, since it is structurally part of the sporophyte, must be grouped by morphology with the other sporophytic structures. But, since the spore is also the first stage of the gametophyte which becomes elaborated through development, it must, by the classification of physiology, be grouped with the gametophyte. The same paradox is to be noted for the fecundated egg. It is quite as distinctly gametophytic from a morphological point of view, but in the physiological sense it is sporophytic.

A consideration of the gametophyte of the Muscineæ reveals to the student its comparatively high structural rank among gametophytes. This high rank is evidenced most particularly by its developing not as a continuous structure with but one developmental stage, but as a discontinuous structure with two distinct developmental stages. While gametophytes above and below the Muscineæ may be considered as generally monomorphic, the gametophyte of the Muscineæ is very constantly dimorphic. It appears in two readily separable stages of certainly deep phylogenetic meaning. The first of these stages is known as protonema. For the second I propose the term, *metanema.* The gametophyte of any hepatic or moss may then be considered as distinguishable into protonema and metanema. Protonemata may be compared with metanemata or with other protonemata, and conversely. An examination of protonemata from the point of view of comparative anatomy shows that they exhibit much power of evolution and improvement. Structurally either filamentous or thalloid, they exhibit much variety, and increase in size and complexity as one passes from the lower Hepaticæ to Hypnum and Bryum. Physiologically they show, in many of the true mosses, wider capacity than in the liverworts, this being particularly evidenced by increase of propagative power with perfecting of propagative apparatus. The protonemal

tubers of *Barbula muralis* and *Trichostomum rigidum* are examples of this increase; and, of a quite different category, the remarkable formation of *protonemal chlamydospores* by *Funaria hygrometrica* should be mentioned.

Similarly one notes in metanemata much development in form and function, as the ascending series from Riccia and Anthoceros is followed. The metanema is, as has been conjectured, very probably a highly specialized gametophore which has assumed in connection with its particular reproductive functions many improvements in vegetative function with their attendant morphological developments. In such plants as Preissia or Conocephalus, where the metanema is differentiated into vegetative and reproductive branches, one sees a reiteration of the process by which the metanema was itself differentiated from the protonema.

The typical metanema of the Muscineæ undergoes a vegetative evolution in two directions. It appears either as thallus or as leafy stem. In the Muscineæ, as far as I know, there is no truly filamentous metanema. The male prothallium of Salvinia, and pollen tubes in general—if they be metanemata at all—would furnish examples of the filamentous type. It is perfectly apparent however that not all of the thalloid metanemata of the Muscineæ are of equal rank. The same is true of the leafy-stemmed metanemata. In the Hepaticæ, where both thalloid and leafy-stemmed metanemata are to be found, some thalli may be regarded as original while others may be considered as derived from leafy stems. Marchantia, for example, may, with much reasonableness, be derived from a Jungermannia archetype; while Anthoceros, on the other hand, may be derived directly from a Coleochæte-like archetype. The close genetic union of Marchantia with Riccia through Boschia and Corsinia, argued by Leitgeb[2] principally upon the basis of sporophytic homologies, is not perhaps to be considered as fully proved. If, on the contrary, Marchantieæ are to be considered rather as reduced Jungermannieæ, the Marchantia thallus may be defined as secondary. Thalli may therefore arise primarily by the evolution of protonemal branches or secondarily by the reduction of a leaf-bearing axis. The same suggestions apply to leafy-stemmed metanemata. They may, like Lejeunea, be considered as having arisen from thalli the margins of which have become dissected;

[2] Leitgeb, Die Marchantieen 49. 1881.

or they may arise directly from protonemal structures, as in Buxbaumia.[3]

One may then classify the metanemal structures of the Muscineæ thus:

Metanema of Muscineæ { Leafy stems { Secondary leafy stems. / Primary leafy stems. ; Thalli { Secondary thalli. / Primary thalli.

It is probable that neither in the Hepaticæ nor in the Musci is there any gametophyte that is not susceptible of division into protonema and metanema. It has been affirmed that Frullania, Anthoceros and a few other Hepaticæ develop directly from the spore as monomorphic structures (Nees ab Esenbeck), but this is not borne out by the researches of Leitgeb[4] who figures for Anthoceros at least a well-marked protonema. And for Frullania and its allies among the foliose Jungermannieæ, while Hofmeister believed that the protonema might be suppressed, the researches of Grönlund[5] have well demonstrated that the protonemal structure is constantly present in one form or another. Leitgeb himself concludes that the protonema is a normal stage for Frullania, Radula and the rest.[6]

Below the Hepaticæ there are undoubted gametophytes without any marked differentiation into protonema and metanema and others in which the differentiation is a matter of grave doubt. Of the first group, Œdogonium and Bulbochæte may be cited; of the second, Chara, Tolypella, Lychnothamnus and their allies. For the gametophytic structure that does not show any differentiation into protonema and metanema and stands lower than the hepatic gametophyte, I propose here the name of *archenema*. The Coleochæte thallus is an example of typical archenema. The gametophyte of the Characeæ is as certainly archenema upon the view that the so-called pro-embryo is an aposporous sporophyte.[7] If however the pro-embryo be taken for protonema and it be assumed that the sporophyte is altogether suppressed, then certainly the mature Chara plant must be classed as metanema.

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[3] Goebel, On the simplest form of moss. Ann of Bot. **6**:355. 1892.

[4] Leitgeb, Die Anthoceroteen. 20. *pl.* 1. 1879.

[5] Grönlund, Mem. sur la germination de quelques hépatiques. Ann. Sci. Nat. Bot. IV. 1:

[6] Leitgeb, Die foliose Jungermannieen 63. 1875.

[7] Vines, The pro-embryo of Chara. Journ. of Bot. 1878.

Three structural categories of gametophytes have now been established in this discussion; archenema, protonema and metanema. The very important question then arises:—what are the homologies of the fern prothallium? It is apparent that there is no *á priori* reason why it may not be any one of the three. In Coleochæte the gametangia are borne upon archenema; in Buxbaumia at least the antheridia are produced upon protonema (Goebel), while in the great majority of Hepaticæ and Musci the gametangia are altogether metanemal in their origin. The fern prothallium might then be considered as a developed Coleochæte-like structure which has not passed through the differentiation into protonema and metanema; or it may be regarded as a thalloid protonema, the metanemal companion stage of which has been suppressed by reduction; or again as a metanema, the embryonal protonemal stage of which has disappeared. It will be seen at once that the correct interpretation of the facts in the case is of great importance. Especially, in view of the fact that there is a modern effort to reach the conclusions of fern phylogeny from the gametophytic as well as from the sporophytic side of the organism, is it imperative that the three possibilities be held distinctly in view. Indeed it would seem as if the criticism here undertaken might indicate the necessity for a revision of some important conclusions which have been put forth recently by students of the Archegoniatæ. For example, I am here strongly inclined to criticise the position maintained by Campbell[8] that "the prothallium of Hymenophyllum corresponds not merely to the protonema of a moss, but to the protonema *plus* the leafy plant." It is not that the position may not be a sound one (for the prothallium may indeed be archenema), but because the verdict should as yet be the Scotch verdict. And especially, in view of the very able and convincing argument of Campbell in favor of considering the eusporangiate ferns as basal and derived from the vicinity of Anthoceros with its undoubted metanema, must one hesitate to regard the prothallium of Hymenophyllum or any other fern as archenemal. But if not archenemal it must apparently correspond with either protonema or metanema. There is of course the possibility of arguing the derivation of the fern prothallium from archenema, and its independent differentiation into protonemal and metanemal stages. The

[8]Campbell, On the affinities of the Filicineæ. Bot. Gaz. **15**: 1. 1890.

prothallia of the Polypodiaceæ, Cyatheaceæ and Schizæaceæ, in which the first product of germination is a filamentous structure afterwards developing into a cordate thallus, or the rather poorly understood prothallia of the Ophioglosseæ may be considered as dimorphic gametophytes and interpreted accordingly. It will be seen, however, that protonemal and metanemal stages would in such case be analogous (not homologous) to the protonema and metanema of the Muscineæ, offering a case of parallel development under similar physiological conditions. And under the methods of classification proposed it is apparent that the conclusions of Goebel[9] can not yet be accepted. As to whether "we may regard as the starting point for Bryophyta and Pteridophyta alga-like forms consisting of branched filaments," judgment must, I believe, be suppressed for the present. It must first be determined whether the prothallium of the fern which is to be taken for the basal fern corresponds with algal archenema or with the protonema or metanema of the Muscineæ.

Conclusion.—The gametophytic structures below the ferns may be described under the heads of archenema, protonema and metanema.

It has not yet been clearly shown with which of these three series the fern prothallium is homologous.

Until the exact homologies of the fern prothallium are discovered, under such a classification it will not be possible to make full use of gametophytic stages in fern phylogenesis.

Phylogenetic argument based upon previous interpretations of the fern gametophyte may be considered as open to possible emendation.

University of Minnesota.

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[9]Goebel, Zur Keimungsgeschichte einiger Farne. Ann. Buitenz. **7**: 74. 1887.